

# AN ENDOPUNCTATE RHYNCHONELLID BRACHIOPOD FROM THE VISÉAN OF BELGIUM AND BRITAIN

by C. H. C. BRUNTON

**ABSTRACT.** The punctate rhynchonellid *Terebratula trilatera* de Koninck is proposed as the type species of a new genus, *Tretorhynchia*. Specimens are described from Viséan rocks of Belgium, the United Kingdom, and from Ireland; their shell structure and intraspecific variation are discussed.

DURING 1969 two specimens of a rhynchonellid brachiopod came to my attention from Viséan rocks of Derbyshire; the first as a museum inquiry, the second from Dr. G. A. Cooper, of the United States National Museum, with whom I had collected specimens at Treak Cliff some months previously. These specimens were unusual in their apparent punctuation. Dr. Cooper remarked (in litt. 1969) that his specimen was not *Rhynchopora*, up till now the only well-known punctate rhynchonellid genus described, and he kindly agreed to let me use his specimen and describe the species.

*Acknowledgements.* I wish to thank the following for their assistance in lending material: Dr. G. A. Cooper, Washington; Mr. M. Mitchell of the Institute of Geological Sciences, Leeds; Mr. C. E. Palmer of the Glasgow Museum; Dr. W. D. I. Rolfe of the Hunterian Museum, Glasgow; and Dr. P. Sartenaer of the Brussels Museum, Belgium. My thanks are also due to my assistant, Mr. A. Rissoné, for technical work, and the Museum's Photographic Studio and Electron Microscope Unit for help in the production of the plates.

Classification and terminology follows the Brachiopoda Treatise (Williams *et al.* 1965).

A search of the material in the British Museum (Natural History) yielded twenty-eight specimens, which are considered to be conspecific, from the Lower Carboniferous of the British Isles, in addition to the ten lent by Dr. Cooper, and the ten lent by the Institute of Geological Sciences, Leeds. Many of these were labelled as *Rhynchonella trilatera* (de Koninck). This species was described by de Koninck (1843, p. 292) from the Lower Carboniferous of Visé, Belgium, and is represented in the Natural History Museum by eight specimens from Belgium, five of which are from de Koninck's collection and two of these still bear the thin blue paper labels given to them by de Koninck himself. One of de Koninck's specimens (B.12642), now in the Davidson Collection, is accompanied by a label in Davidson's writing, which reads: '*Rhynch. trilatera*. de Kon. Carb. Limestone Visé, Belgium. Sent to me by De Koninck as his type and for comparison with English specimens' (Pl. 11, figs. 5, 6). These fifty-six specimens form the basis of this study which aims at deciding the relationships of the British specimens with *R. trilatera* (de Koninck) from Belgium, elucidating the nature of the apparent punctuation of the shell, and deciding upon the taxonomic position of the British and Belgian specimens.

To assist in this study portions of shell and complete specimens have been studied both optically and by scanning electron microscope (Pl. 11, figs. 7-14). All fifty-four

specimens in which the brachial valve is complete (commonly the tip of the pedicle valve umbo is broken), have been measured and counts of ribbing on the brachial valves noted. This data has been plotted graphically and, where the number of specimens has allowed, it has been treated statistically in order to investigate variation between the Belgian, British, and Irish specimens (Tables 1–3). Finally, two specimens have been sectioned serially in order to discover the internal hinge and crural structures (text-figs. 1–12), using a lathe grinder (Hendry, Rowell, and Stanley 1963).

#### *Relationships between the British and Belgian specimens*

De Koninck (1843, p. 292, pl. 14, figs. 7a–d) described *Terebratula trilatera* from the Carboniferous Limestone of Visé as rare. He stressed the resemblance in shape to an isosceles triangle and stated that his species had 18–22 angular ribs. In these characteristics, and other respects, his description is adequate for most of the British material. However, he made no comment as to the nature of the shell substance and the relative dimensions cited, as well as those of the figured specimen, differ from those typical of British specimens in being longer than wide and thicker relative to length. Later, in 1887, de Koninck redescribed his species giving dimensions which accord closely with those of the specimens from Britain; the length and width being given as equal and the thickness as 64% of these dimensions. Fortunately the situation is relieved further by having four well-authenticated specimens named *trilatera* by de Koninck and a fifth almost certainly from his collection. In all known respects these specimens match with the British material and the two groups of specimens are considered to be conspecific. Unfortunately, the number of specimens available from Belgium is insufficient to test for significance in difference between their growth axes and those obtainable from British specimens. Graphical plotting suggests that there would be no significant difference (text-figs. 13–15).

#### *Shell structure*

In assembling the material studied an important criterion was the apparent shell punctation. This feature, previously noted by Dr. Cooper and myself, has given impetus to the investigation and, together with its outline, makes *Terebratula trilatera* an easy species to recognize. From low-power optical inspection, at  $\times 30$ , it is clear that the shell substance is patterned by minute outwardly projecting protuberances evenly spaced throughout the secondary shell layer with a frequency of from 150 to 180 per  $\text{mm}^2$ . Rarely, on exfoliated shell near the inner surface of the valve, the protuberances are dark at the centre, as if filled with fine sediment. After ultrasonic cleaning minute pores can be distinguished penetrating these structures. At magnifications of from one to two thousand, using a scanning electron microscope, it is clear that the fibres of the secondary shell layer are bent outwards around a central hole (Pl. 11, figs. 8, 10, 13), just as in living punctate brachiopods, and that the shell substance of this species can be described as endopunctate. It is possible to find patches of well differentiated non-fibrous outer primary layer (Pl. 11, figs. 9, 10), as in living brachiopods, on only a few specimens. In such areas the punctae are difficult to distinguish owing to the fact that they terminate close to the junction between the primary and secondary shell layers. This is unlike living punctate brachiopods in which the punctae extend well into the primary layer and

are capped by thin 'canopies' of primary shell through which the 'brush' extended (Owen and Williams 1969). It has not been possible to distinguish canals, which might have accommodated the 'brush', within the primary layer above the punctae of *T. trilatera*, and this adds to the difficulty of recognizing punctae where primary shell is preserved. Commonly sediment within the punctae and slight recrystallization of the surrounding shell obscures the punctal cavity. However, inspection of cellulose acetate peels taken from various layers of the shell of *T. trilatera* and the punctate terebratulide *Dielasma*, from similar Viséan lithologies, provides convincing evidence of both having shells with similarly concentrated punctae and associated features of shell micro-structure.

Thus, we now know that the specimens may be assigned to de Koninck's species *trilatera* and that this species is endopunctate. The remaining problem is its taxonomic position. Presently the only well-known punctate genus of the Rhynchonellida is *Rhynchopora*, erected by W. King in 1865 when describing the punctate shell *Terebratula geinitziana* de Verneuil from Permian rocks of Russia. This genus is characterized by its dorsibiconvexity and by having a strong fold and sulcus in the brachial and pedicle valves respectively; the anterior commissure is strongly folded by a linguiform extension of the pedicle valve. These features contrast with *T. trilatera* and led Dr. Cooper to remark that the Treak Cliff specimens in his collection could not be assigned to *Rhynchopora*.

Muir-Wood (1955, p. 74) discussed the genus, pointing out that the species assigned are widely distributed throughout Carboniferous and Permian rocks and that they 'belong to more than one genus'. Drot (1964) described a new Famennian species, from Morocco as *Rhynchopora morini*, which seems to be punctate but differs from *Rhynchopora geinitziana* in details of external morphology.

The small endopunctate species *Rhynchopora youngii* Davidson (1880, p. 286) has a strongly folded commissure and ribs that do not arise from the umbones; it was reported, in Davidson, from Upper Viséan and Lower Namurian rocks of the Dalry area, Ayrshire. This species is quite unlike *T. trilatera* and although it also differs from the type species of *Rhynchopora* in its ribbing, it is related more closely to that genus than to *Tretorhynchia*, the new genus erected herein. It appears to be a rare species, only being known to the author by ten specimens in the Young Collection (seven in the Hunterian Museum, Glasgow, and three, figured by Davidson, in the Glasgow Art Gallery and Museum). Two other reportedly punctate species of *Rhynchopora* from Lower Carboniferous, Viséan, rocks are *R. deltoidea* Reed (1954, p. 188) and *R. longa* Afanas'yeva (1969, p. 62); the former from the Lower Limestone Group of east Scotland and the latter from the Onon River, Transbaykalia S.S.R. Both species are longer than wide and sulcate, and appear reasonably to have been assigned to *Rhynchopora*.

A poorly understood genus, which might be punctate, is *Paryphorhynchopora* Simorin (1956, p. 245), based upon *Pugnoides korsakpaica* Nalivkin 1937, from Tournaisian strata in north-east Kazakhstan, U.S.S.R. Nalivkin made no mention of a punctate structure, but Simorin wrote of the valves being covered by rows of minute, closely spaced, slightly elongate pores giving the impression of fine radial striations like those of *Paryphorhynchus* Weller 1914 (= *Paraphorhynchus* Weller 1905). Simorin briefly compared his genus with *Rhynchopora*, saying that the shape and arrangement of the pores differs. Unfortunately, neither the illustrations of Simorin nor of Nalivkin are good



enough to be sure of recognizing punctation. However, it seems likely that the rows of fine pores described may be no more than surface ornamentation, as in *Porostictia* Cooper (1955), based upon the Upper Devonian species *Paraphorhynchus perchaensis* Stainbrook 1947 from New Mexico; in this species, the 'pores' are surface elongate pits which do not penetrate the shell. Thus, in the absence of full information on *Paryphorhynchopora*, it is impossible to know if some Devonian and Lower Carboniferous seemingly punctate species should be assigned to this genus or not. However, whatever the true nature of the shell of *Paryphorhynchopora* the external morphology is quite unlike that of de Koninck's species and it seems necessary, therefore, to erect a new genus based upon *T. trilatera* de Koninck.

Dunbar and Condra (1932, p. 295) argued that the North American Pennsylvanian species they assigned to *Rhynchopora* indicated that this genus should be placed in the Terebratulida, perhaps within the Centronellidae. Sections of their specimens reveal a posteriorly perforated hinge plate covering a cavity between it and the septalium. These structures, the punctation, and the vertically disposed blade-like brachial supports led Dunbar and Condra to exclude their material from the Rhynchonellida. The internal structures of the American species *Rhynchopora hamburgensis* Weller and *R. pustulosa* (White) described by Dunbar and Condra, and *R. magnicosta* Mather, described by Weller in 1914 as rhynchonellid, differ from those of *T. trilatera*, whose cardinalia is not unlike that of some terebratulids such as the Permian genus *Yochelsonia*.

Punctation of the brachiopod shell has evolved and been lost from various brachiopod stocks during Phanerozoic time and it does not seem too unlikely that the Rhynchoporidae should be the sole punctate family of rhynchonellids. Furthermore, as is shown herein, the punctation of *T. trilatera* differs in detail from that normal for Terebratulida. There is no evidence as yet for the brachiophore supports being in the form of a loop, as in the Terebratulida.

Order RHYNCHONELLIDA Kuhn 1949  
 Superfamily RHYNCHOPORACEA Muir-Wood 1955  
 Family RHYNCHOPORIDAE Muir-Wood 1955  
 Genus TRETORHYNCHIA nov.

*Type species. Terebratula trilatera* de Koninck 1843.

*Diagnosis.* Rhynchoporidae approximating an equilateral triangle in outline, with bi-convex lateral profile and lacking fold in anterior commissure. Typically 18–22 persistent costae. Septalium and strong socket ridges; dental plates delicate and close to sides of valve.

*Range.* Lower Carboniferous, middle to upper Viséan.

*Discussion.* At present only the type species is assigned to this genus. In outline and profile it is similar to some tetracamerids, but differs in lacking either a folded margin or complex dental plates, and in being endopunctate. *Pseudowellera* is similar in its persistent costae and approaches a triangular outline, but it is sulcate, has truncated antero-lateral corners and is impunctate. The generic name is derived from 'tretos'—a Greek word meaning perforated—combined with the root of *Rhynchonella*.

*Tretorhynchia trilatera* (de Koninck)

Plates 11 and 12

- 1843 *Terebratulina trilatera* de Koninck, p. 292, pl. 14, figs. 7a-d.  
 1861 *Rhynchonella? trilatera* (de Koninck); Davidson, p. 109, pl. 24, figs. 23-6.  
 ?1861 *Rhynchonella pleurodon* Phillips; Davidson, pl. 23, fig. 10a.  
 1887 *Rhynchonella trilatera* (de Koninck); de Koninck, p. 50, pl. 16, figs. 68-83.

*Diagnosis.* Outline approximating an equilateral triangle, with rounded antero-lateral margins and pointed umbones. Postero-lateral flanks flattened; lateral profile variable but mean thickness approximately five-eighths mean width. Both valves slightly sulcate posteriorly. Anterior commissure not folded. Commonly 18-22 strong angular costae on brachial valves, normally seven in 4 mm at 4 mm from dorsal umbo. Pedicle valve with median rib. Brachial valve interior with short low median septum supporting septalium and with deep crura. Pedicle valve with short thin dental plates. Shell substance normal but finely endopunctate.

*Type specimen.* I am told by Dr. Vandercammen (in litt. November 1969), of the Institut Royal des Sciences Naturelles, Belgium, that his institution has no type specimens of *T. trilatera* de Koninck, nor specimens that can be said with any certainty to have been figured by de Koninck in 1843. The Brussels museum does, however, have five specimens figured by de Koninck in 1887, and Dr. Sartenaer has been kind enough to lend me three of them from which to choose the type. The type specimen here chosen is no. I.G. 2738b (Pl. 11, figs. 1-4), figured by de Koninck in 1887, pl. 16, figs. 69-75; it cannot be designated as lectotype because it is not demonstrably one upon which de Koninck based his description in 1843. This specimen is unusually wide compared to its length, but in other respects is like the majority of specimens studied. Some endopunctate shell material is preserved and dental plates are visible within the ventral umbo.

*Other material.* In the British Museum of Natural History: four specimens from the de Koninck Collection from Viséan rocks of Belgium; four specimens from the Viséan (B<sub>2</sub>) of the Treak Cliff, Castleton area, Derbyshire; eight from the Viséan of Wetton, Staffordshire; four specimens from the Viséan of Anglesey; four specimens from Bolland, and three from Settle, Yorkshire, probably also Viséan; four specimens from Lower Carboniferous rocks of the Cork area, Ireland. Lent by the Institute of Geological Sciences, Leeds: four specimens from the Viséan (B<sub>2</sub>) of the Treak Cliff area; two from Castleton; one from Narrowdale, Derbyshire; three from Alstonfield, Derbyshire (referred to by Davidson 1861 and forming the basis of his illustrations on pl. 24, fig. 26); all these from Viséan rocks. Lent by the Smithsonian Institution, Washington: ten specimens from the Viséan (B<sub>2</sub>) of Treak Cliff, Derbyshire.

*Description.* The species is markedly triangular in outline with maximum width occurring at about three-quarters of the length of the shell. Mean width slightly exceeds mean length in the Belgian and British specimens. The anterior margin may be straight or slightly convex or concave medianly. The variable thickness correlates more closely with length than with width (Table 1). The flanks are flattened, but posteriorly the commissure protrudes at a rudimentary hinge line (Pl. 12, fig. 9). The brachial valve median sulcation follows the line of the median septum (Pl. 11, fig. 5) and on this valve 18-22 persistent costae are commonly developed; these widen anteriorly but they diminish in size laterally. On pedicle valves there is a median costa; on brachial valves a pair of submedian costae so that the total number of dorsal costae is commonly an even number

(Table 2). On only two specimens subequal branching of costae on the brachial valves led to the development of costellae nearly equal in size to the parent costae. Naturally, on the pedicle valve a corresponding intercalation of a costella occurred. The pedicle valve interior has short thin dental plates which do not continue anteriorly as ridges on the floor of the valve. The teeth are large, extending dorso-medially for about two-thirds of the valve width (at that particular distance from the umbo; text-fig. 4). The brachial valve interior has a median septum, about 2 mm long, which posteriorly forms a septalium by fusion with short crural plates. Crura are distally narrow but deep and

TABLE 1. Statistics of length (*l*) and width (*w*) of brachial valves, and shell thickness (*th*) of *T. trilatera* specimens from the United Kingdom, Belgium and Ireland. The arithmetic coefficients of correlation (*r*) are given for parameters where the number of specimens is sufficient

	United Kingdom	Belgium	Ireland
$\bar{l}$ (var.)	= 8.99 (2.725)	6.81 (3.630)	8.28 (1.325)
$\bar{w}$ (var.)	= 9.48 (3.221)	7.43 (1.646)	6.90 (0.865)
$\bar{th}$ (var.)	= 5.82 (2.254)	4.52 (2.720)	4.64 (0.832)
<i>r</i> for <i>l/w</i>	= 0.848		
<i>r</i> for <i>l/th</i>	= 0.769		
<i>r</i> for <i>w/th</i>	= 0.674		
<i>n</i>	= 43	6	5

arise from the anterior ends of the large inner socket ridges (text-fig. 16). In the sectioned specimens the anterior tips of the crura may be broken, so their length may have been greater than indicated by the serial sections.

*Discussion.* The species is distinctive in many respects. Internally, the articulation is unusually strongly developed (perhaps a characteristic linked with the lack of commissural folding which normally, in rhynchonellaceans, assists in the fit of one valve with another) so that large inner socket ridges are present. The crura appear to extend

#### EXPLANATION OF PLATE 11

*Tretorhynchia trilatera* (de Koninck), Lower Carboniferous, Viséan.

Figs. 1–4. Ventral, dorsal, anterior ( $\times 2.6$ ) and posterior ( $\times 3.8$ ) views of the type specimen from Visé, Belgium, De Koninck Collection, IRSN, no. I.G. 2738b.

Figs. 5, 6. Dorsal ( $\times 5$ ) and posterior ( $\times 20$ ) views of an internal cast from Visé, Belgium, showing the positions of the dental plates and cardinalia. B 12642.

Figs. 7–14. 'Stereoscan' scanning electron micrographs of specimens coated with gold. 7. Composite ventro-lateral view of a young specimen from Llanfair, Anglesey, showing the shell ornamentation at  $\times 10$ . BB 58456. 8–12. Details of the shell structure as illustrated by the I.G.S., Leeds, specimen no. 55 from Alstonfield, Derbyshire (see Pl. 12, figs. 8, 9). The outer surface of the specimen is towards the top of each figure. Figs. 8–10 illustrate the junction of the primary to secondary shell, and the distribution of punctae within the secondary shell  $\times 300$ . Figs. 11, 12 detail punctae well within the secondary layer and at their distal ends, close to the inner surface of the primary layer, where they become capped by shell.  $\times 600$ .

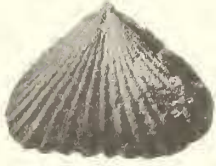
Figs. 13, 14. Details of the punctae in the specimen shown on fig. 7 in which some recrystallization of the shell has occurred. However, flexure of the secondary fibres around the punctae can be distinguished.  $\times 1000$ .

IRSN = Institut Royal des Sciences Naturelles, Brussels.





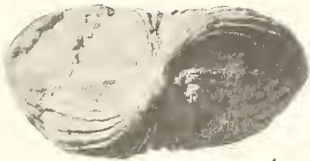
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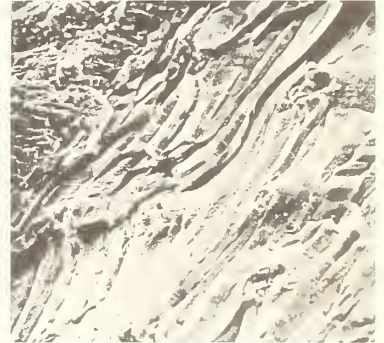
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12



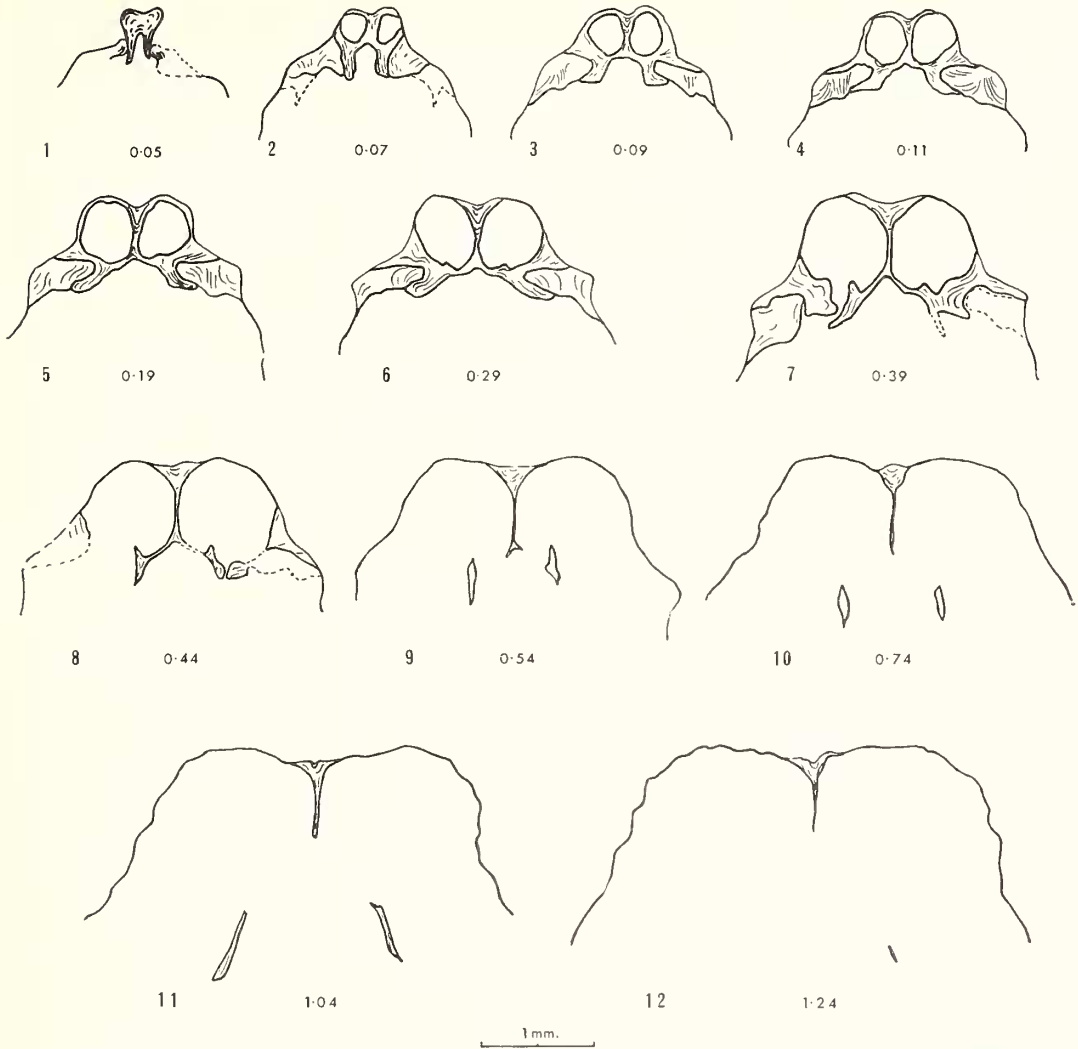
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14







TEXT-FIGS. 1-12. Transverse serial-sections through *T. trilaterra* (IGS, Leeds specimen RS 3750 from B<sub>2</sub> reef limestones, Odin Fissure, north end of Treak Cliff, Derbyshire) showing the internal structures. Much of the external shell substance was missing prior to sectioning. Distances from the brachial valve umbo are given in mm.

from the anterior end of these ridges making it impossible to differentiate either the outer hinge plates from inner socket ridges or the crural bases from the inner hinge plates, which fuse medially on to the median septum. Owing to a shortage of material only two specimens were serially sectioned and the pedicle valve umbones were missing. No cardinal process has been recognized in section, and from the internal mould (Pl. 11, fig. 6) this structure was not developed.

In comparing the external morphology of the specimens from Belgium, the United Kingdom, and Ireland it is clear that the Irish specimens from the Cork district differ

TABLE 2. The total number of ribs counted on 54 brachial valves of *T. trilaterra* from the United Kingdom, Belgium, and Ireland

Ribs	16	17	18	19	20	21	22	23	24	
United Kingdom	4	2	13	4	10	1	6	0	3	43
Belgium	0	0	2	0	3	0	1	0	0	6
Ireland	2	0	1	1	1	0	0	0	0	5
	6	2	16	5	14	1	7	0	3	54

TABLE 3. The number of ribs counted in a width of 4 mm at a distance of 4 mm from the dorsal umbones of *T. trilaterra* from the United Kingdom, Belgium, and Ireland

Ribs	6	7	8	9	10	
United Kingdom	10	18	9	3	2	42
Belgium	1	1	2	0	1	5
Ireland	1	1	1	0	2	5
	12	20	12	3	5	52

## EXPLANATION OF PLATE 12

*Tretorhynchia trilaterra* (de Koninck), Lower Carboniferous.

Figs. 1–4. Dorsal, lateral ( $\times 3.0$ ) ventral and anterior ( $\times 2.7$ ) views of a typically shaped specimen (in dimensions close to those given by de Koninck in 1887) from Wetton, Staffordshire. Davidson Collection. BB 58455.

Figs. 5–7. Lateral, dorsal and ventral views ( $\times 2.5$ ) of a specimen from Alstonfield, Derbyshire, referred to by Davidson (1861) and almost certainly used in his figures of pl. 24. GSL 54.

Figs. 8, 9. Anterior and dorsal views ( $\times 2.7$ ) of a second specimen from Alstonfield, Derbyshire and figured by Davidson (1861, pl. 24, figs. 26). GSL 55. The above two specimens illustrate the short but relatively fat variants of the species. Specimen 55 has an unusually wide hinge line.

Figs. 10–12. Dorsal, ventral and lateral views ( $\times 3.5$ ) of a specimen from Little Island, Co. Cork, Eire. J. Wright Collection. BB 58457.

Figs. 13–15. Dorsal, ventral and lateral views ( $\times 3.5$ ) of an elongate, fat specimen from Little Island, Co. Cork. J. Wright Collection. BB 58458.

Figs. 16–18. Dorsal, ventral and lateral views ( $\times 2.7$ ) of a broad, thin specimen from Bolland, Yorkshire. Gilbertson Collection. BB 58461.

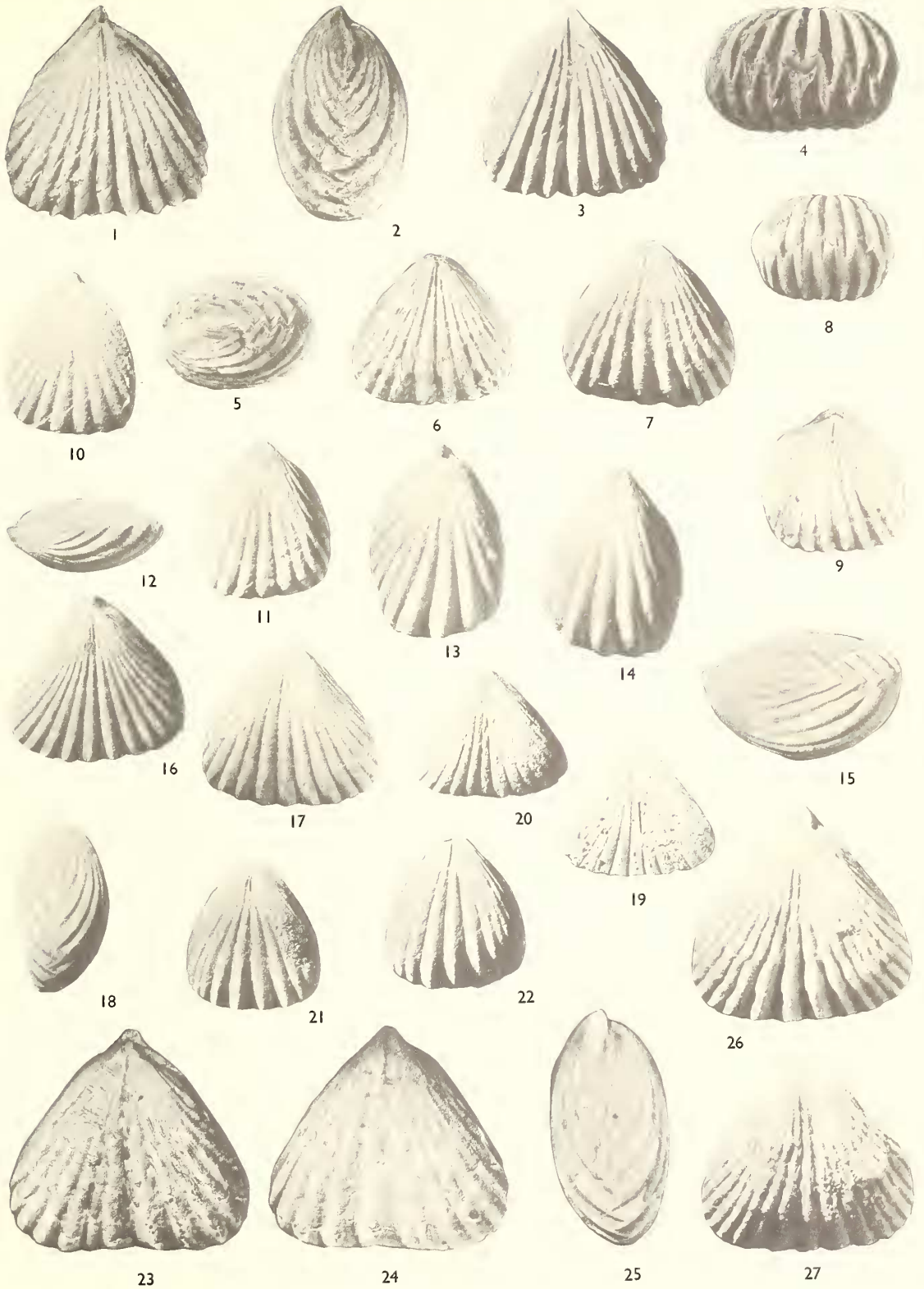
Figs. 19, 20. Dorsal and ventral views ( $\times 2.5$ ) of a thin specimen from the north end of Treak Cliff, Castleton, Derbyshire. Collected Cooper and Brunton. USNM, Washington.

Figs. 21, 22. Dorsal and ventral views ( $\times 2.5$ ) of a thick specimen collected with that illustrated in figs. 19, 20. USNM, Washington.

Figs. 23–25. Dorsal, ventral and lateral views ( $\times 6$ ) of a young specimen from Settle, Yorkshire. Growth lines and shell ornamentation are distinguishable. Davidson Collection. BB 58459.

Figs. 26, 27. Dorsal and ventral views ( $\times 4$ ) of a larger specimen from Settle. Davidson Collection. BB 58460.

GSL—Geological Survey, Leeds. USNM—United States National Museum. All other specimens in British Museum (Natural History).



BRUNTON, Carboniferous endopunctate rhynchonellid



